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# Scyllarid lobster biology and ecology

Chapter

# Scyllarid Lobster Biology and Ecology

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## Abstract

The family Scyllaridae is the most speciose and diverse of all families of marine lobsters. Slipper lobsters are found in both tropical and temperate habitats with hard or soft substrates and at different depths, and exhibit a wide array of morphological, anatomical, and physiological adaptations. Among the 20 genera and at least 89 species constituting 4 subfamilies, only some members of 4 genera, *Thenus* (Theninae), *Scyllarides* (Arctidinae), *Ibacus* and *Parribacus* (Ibacinae), form significant fisheries because of their large size. While scientific information on these lobsters has increased considerably in recent decades, it is still limited compared with commercially valuable spiny and clawed lobsters, and is confined to a few key species. The present chapter presents the current available knowledge on the biology of scyllarids and attempts to point out where questions remain to help focus further studies in this important group.

**Keywords:** slipper lobsters, Scyllaridae, taxonomy, genetics, anatomy, physiology, ecology, life history, behavior, fisheries

## 1. Introduction

Slipper lobsters, family Scyllaridae (Latreille, 1825) have been known and described since the late 1700s and are considered part of the superfamily Palinuroidea that consists of spiny lobsters (Palinuridae), furry lobsters (Synaxidae), blind claw-footed lobsters (Polychelidae), and slipper or shovel-nosed or bulldozer lobsters (Scyllaridae) [1, 2]. The Scyllaridae are organized into four subfamilies (Ibacinae, Arctidiane, Scyllarinae, and Theninae) and comprise 20 genera with at least 89 extant species thus far recognized [3–6].

Only four genera—*Scyllarides* (Arctidinae), *Ibacus* and *Parribacus* (Ibacinae), and *Thenus* (Theninae)—form any kind of significant fishery because these individual species tend to be large in size [7]. Of these four genera, *Scyllarides* (Gill, 1898) has been studied extensively due to their large adult size, which makes them economically important; their worldwide geographical distribution in tropical and subtropical habitats; and their numerous species (14) [1]. Considerable knowledge is also available for species within the genus *Thenus* because of some relevance in certain fisheries as well as the success in rearing these animals in aquaculture [8]. Research on other species generally arises with overfishing of and a shift away from sister species (generally palinurids) and thus always lags behind exploitation, which is problematic for the creation of sustainable fisheries. Although small in size, lobsters of the genus *Scyllarus* often become a minor target for fisheries (e.g., [9, 10]).

The present review is an attempt to summarize the somewhat patchy information available in the scientific literature on scyllarids. In addition, expanding our knowledge on slipper lobsters may prove beneficial to humans in ways beyond providing a food source, given that large proteins recently isolated from *Ibacus novemdentatus* have displayed cytotoxic activity against human cancer cells [11].

## 2. Taxonomy, phylogeny and evolution

Lobsters were significantly more diverse in the Mesozoic, especially during the Triassic and Jurassic, than in the Cenozoic and Holocene. The Achelata appeared 391–351 million years ago (MYA), but did not diverge into the palinurid and scyllarid lineages until the Permian (~250 MYA) [12, 13]. Fossil remains of scyllarids date back to the mid-Cretaceous (100–120 MYA) [3], but are not well-represented since their fossils come mostly from low energy (shale, clay, ironstone) or lithographic (limestone) deposits [14–16]. Today's scyllarids live in different habitats (coral and sponge reefs, and medium to high energy environments) from fossil forms, but the sparse fossil record of this group makes it difficult to speculate on when their habitat shift occurred, although their major radiation began in the Late Jurassic and continued through the Holocene [14].

Slipper lobsters are closely related to the Palinuridae and Synaxidae, all of which comprise the Achelata; they share numerous characters, most notably their unique larval phase (i.e., phyllosoma) which separate the Achelata from all other Decapoda [3]. The plate-like antennal flagellum of slipper lobsters is a highly derived feature that is common to all 89 species and distinguishes them from the palinurids and synaxids which possess whip-like antennae. The Scyllaridae underwent considerable taxonomic revision from 1991 to 2002, mostly within the Scyllarinae, and now consist of 20 genera. The highest taxonomic diversity is among the smaller species [1, 17].

The subfamily Arctidinae consists of 2 genera and 17 species. These are some of the larger scyllarids. *Arctides* and *Scyllarides* species typically have a highly vaulted carapace, a three-segmented mandibular palp, and a shallow cervical incision along the lateral margin of the carapace. The subfamily Ibacinae consists of 3 genera, *Evibacus, Ibacus* and *Parribacus*, with a total of 15 species. In these species, the carapace is significantly dorso-ventrally compressed with a deep cervical incision along the lateral margin of the carapace. The mandibular palp is simple or two-segmented, in contrast to the Arctidinae. One genus, *Thenus*, and five species are recognized presently in the subfamily Theninae [5]. The Theninae display extremes: the body is highly flattened and their eye orbits are found at the extreme antero-lateral extent of the carapace. In contrast, the 52 species of Scyllarinae found within 14 genera all have vaulted carapaces covered with tubercles and their eyes are more medial in placement. Yet both Theninae and Scyllarinae lack a flagellum on the exopod of the first and third maxillipeds [18]. See **Figure 1** for representatives of these species and **Figure 2** for examples of scyllarid mouthparts.

The taxonomy of Scyllaridae is based mainly on the morphology of the adults and to lesser extent of that of their pelagic larvae, the phylosomas. Recently molecular genetic tools have been used to assess taxonomic and phylogenetic issues, and the main clades found within Scyllaridae are in agreement [13] with current taxonomy based on adult morphology [1, 19, 20] and recent molecular studies [5]. All subfamilies (Arctidinae, Theninae and Scyllarinae) are now considered monophyletic, except for the Ibacinae [5]; this contrasts with a more recent analysis [21] that concluded that the Scyllaridae are fully monophyletic. The Arctidinae appears to represent the earliest branching lineage during the evolution of this group [5], which corresponds to the fossil record. In addition, slipper lobsters have likely evolved from shallow (onshore)

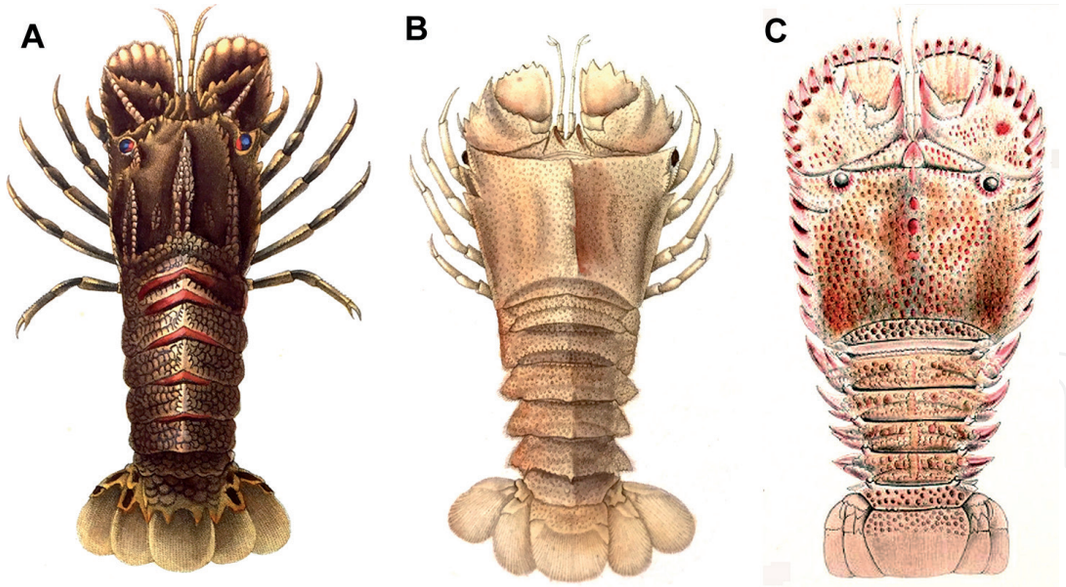


**Figure 1.**
*Different forms of scyllarid lobsters. (A) Scyllarus arctus; (B) Thenus orientalis; (C) Parribacus antarcticus. A and B from Cuvier G. Le Règne animal: D'Après son organization, pour Sevir de base a L'Histoire Naturelle des Animaux, et D'Introduction a L'Anatomie Comparèe. Accompagnée de planches Gravées. Imprime chez Paul Renouard, Paris, France, 1837; C from Dana JD. United States exploring expedition during the years 1838, 1839, 1840, 1841, 1842 under the command of Charles Wilkes, U.S.N., Vol. XIII. Crustacea. C. Sherman, Philadelphia, 1852.*

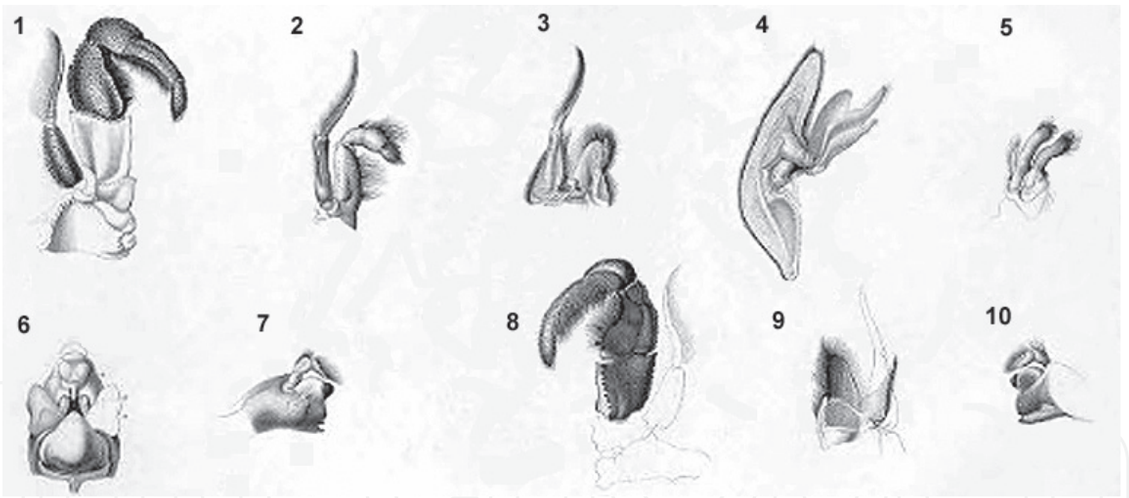


**Figure 2.**
*Scyllarid mouthparts. (1) Aboral/ventral view of third maxilliped; (2) aboral/ventral view of second maxilliped; (3) aboral/ventral view of first maxilliped; (4) aboral/ventral view of second maxilla; (5) aboral/ventral view of first maxilla; (6) mouth; (7) aboral/ventral view of mandible; (8) oral/dorsal view of third maxilliped; (9) oral/dorsal view of first maxilliped; (10) oral/dorsal view of mandible. From Savigny, J-Cés. Iconographie des Crustacés et des Arachnides de l'Égypte. De l'Imprimerie Royale, Paris, France; 1805.*

to deep water (offshore) species [5]. These same molecular tools suggest that two Atlantic species, *Scyllarus depressus* and *S. subarctus*, are a strongly supported clade with low genetic differentiation, indicative of a recent split into sister taxa [22].

## 3. Life history

The life history of scyllarids parallels that of palinurids and can be divided into a series of developmental phases. These lobsters typically begin their pelagic lives

as phyllosoma larvae (**Figure 3**), although some scyllarids (*Scyllarides aequinoctialis* [23, 24], *S. herklotsi* [25], *S. latus* [26], *Ibacus alticrenatus* [27] and *I. ciliates* [28] or *I. novemdentatus* [19]) hatch as a naupliosoma (pre-larva), a short-lived form lasting a few hours that bears only the first three pairs of cephalic appendages [29]. Abdominal appendages are typically absent or rudimentary in early phyllosomas, but appear in later stages [30]. Exopodites are found on all thoracic appendages of phyllosoma larvae until their metamorphic molt when they are lost from all but the first and second maxillipeds; here exopodites are retained and used for generating currents around the mouth region [31]. Scyllarid phyllosomas deviate from other decapod larvae in that they are missing a fully developed exopod on the third maxilliped and this may indicate a phylogenetic separation of feeding strategy [3].

The dispersal of phyllosomas varies among species and depends largely on whether the parental stock is found within lagoons formed by coral island barrier reefs or in deeper waters [32–36]. Those hatched in coastal lagoons tend to remain there, while those hatched in deeper water gradually move shoreward, such that final-stage phyllosomas are found much closer to shore [30]. Some phyllosomas undertake diel vertical migrations, but data are limited as to the extent of these migrations and the species-specific preferences for various depths [30, 37] as well as the efficacy of their swimming behavior. It is likely that smaller instars vertically migrate less than later, larger instars [35] and may use passive transport by occupying vertical strata that move them in specific directions [30]. Some phyllosomas even travel attached to the aboral surface of jellyfish medusae or siphonophores [38–41], which may affect larval dispersal or allow them to remain relatively near shore [29, 30]. Understanding of phyllosoma behavior and dispersion has been challenged by the ability to correctly identify species; however, recent use of molecular genetics and DNA barcoding is improving the ability to make species identification possible in the field [42, 43].

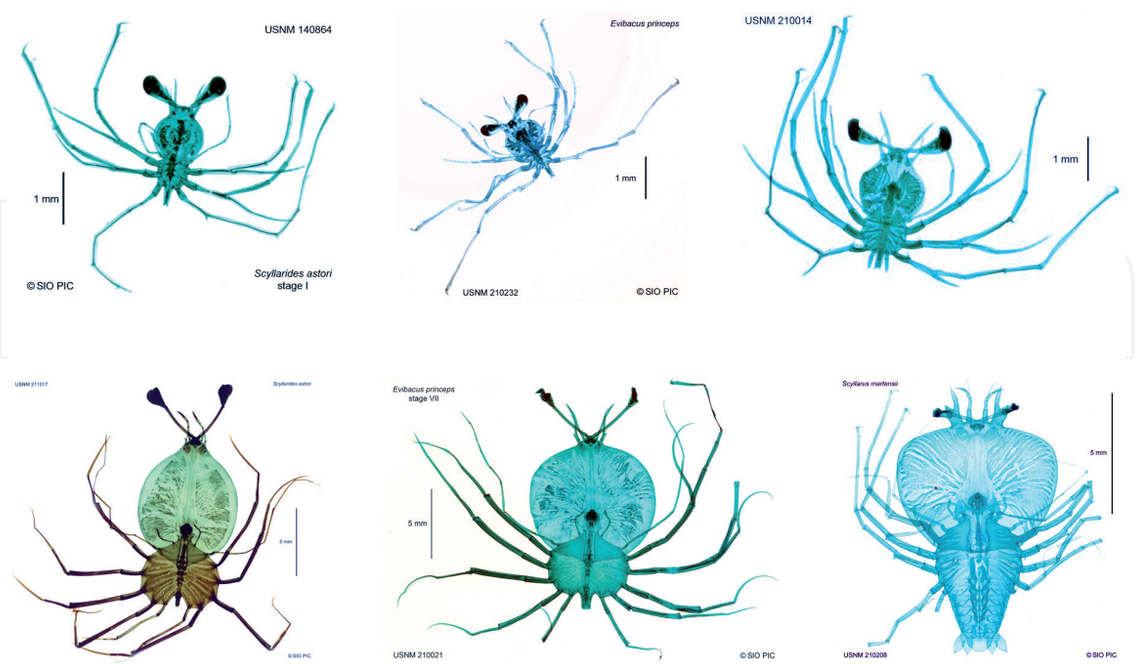


**Figure 3.**
*Various stages of scyllarid phyllosoma larvae. Top, early stages of Scyllarides astori and Evibacus princeps. Bottom, later stages of S. astori, E. princeps, and Scyllarus martensii. From the Martin Wiggo Johnson Phyllosoma slide collection of the Scripps Institute of Oceanography Pelagic Invertebrate Collection website (https://scripps.ucsd.edu/collections/pi/overview/collection-databases-zooplankton-guide/m-w-johnson-lobster-phyllosoma-slide).*

Phyllosomas are raptorial feeders, using their pereiopods to grasp onto food items, which are then shredded by the maxillipeds and masticated by molar processes of the mandibles [44]. Mostly fleshy foods are ingested; such food types are more readily available in coastal waters than in offshore, oligotrophic waters [29, 30, 45]. Some scyllarid phyllosomas have been observed clinging onto or "riding" the medusa stage of some gelatinous zooplankton. For example, a recent report of a videotaped scyllarid lobster phyllosoma swimming while dragging a prayid siphonophore behind it suggests that gelatinous forms may serve as a critical food and/or defense against predation (by ingestion of the nematocysts) and refutes the idea that hitching a ride on these organisms is energy-saving due to passive transportation [41]. Recently, molecular methods using the central domain of the 18SrDNA gene have identified food items of some species of scyllarid and palinurid phyllosomas and suggest that these forms feed on appendicularians, salps, and cnidarians [46]. Ctenophores fed to phyllosomas of *Thenus orientalis* are accepted readily and provide nutritional support [47] and similar results were obtained with the phyllosomas of *T. australiensis*, *Ibacus novemdentatus*, *I. ciliatus* fed on jellyfish [48–51]. Some species of wild phyllosomas were found to contain cnidarian tissue in their hepatopancreas and feces, and these phyllosomas seem capable of encapsulating nematocysts [52] suggesting that these larvae utilize jellyfish as a food source. Few studies have examined exactly how phyllosomas consume jellyfish, but one possible mechanism is for phyllosomas to cling onto the exumbrella, feed on tentacles or oral arms first, and then consume the exumbrella [48, 53]. Phyllosomas riding on jellyfish manage to groom and clear mucus extruded by jellyfish to dampen microbial growth on their bodies [54].

The final-stage phyllosoma molts into the highly specialized nisto (see **Figure 4**), or post-larval stage, which, like their spiny lobster (pueruli) and clawed lobster (post-larvae) counterparts, utilize surface waters to swim toward benthic habitats to settle. Nistos are neither completely planktonic nor completely benthic—they are caught in plankton tows demonstrating that they are pelagic at least part of the time [29]. In many species of scyllarids, the nisto appears to bury into soft substrates during the day and swim actively at night; some species even change coloration daily between these two habitats to remain cryptically colored in both environments [29]. Some scyllarid nistos are excellent swimmers (using their abdominal pleopods), while others are poor swimmers; some are also capable of executing tail flips (backward swimming) as a means of escape [55]. These swimming differences may exist due to marked differences in the size of pleopods among different species [56]. However, this suggestion has not been adequately tested.

As with spiny lobster pueruli, the nisto appears to rely on energy reserves, rather than to actively feed [30], although the structure of the proventriculus is transitional between the phyllosoma and the juvenile [57] which suggests that it can process and sort food particles at this stage of development. The nisto also bears a cardio-pyloric valve that divides the anterior and posterior cardiac chambers, but lacks a gastric mill. Thus, if food is consumed by the nisto, it is likely soft and processed mainly by the mouthparts prior to ingestion [57]. Nistos appear similar in form to juveniles and bear the derived feature of flattened antennae, but are transparent instead of being reddish-brown. Their abdominal pleopods still bear swimming (natatory) setae [58] to aid in transitioning them from the pelagic to the benthic realm.

Juvenile life history of scyllarids is lacking for all species except those that have been successfully reared in culture (e.g., *Thenus* species [59] or *Ibacus* species [49, 60, 61]). This primarily is the result of a problem in sampling and not knowing where juvenile grounds lay. For example, in *S. latus* no live juvenile or nisto of the

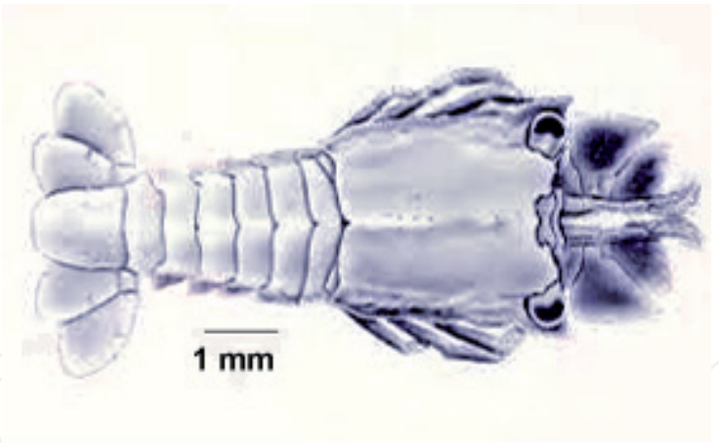


**Figure 4.**
*Nisto of Scyllarus americanus (Top). From Ref. [23]. Open access: https://archive.org/details/larvaldevelopmenoorobe. Nisto of unidentified scyllarid species in Florida waters (Bottom). Photo by Casey Butler.*

commercially exploited Mediterranean slipper lobster, *Scyllarides latus* (Latreille, 1851), had ever been sampled despite ample information available on the ecology and behavior of adults of this species [62]. Museum surveys of invertebrate collections provided a small specimen of *S. latus* (36 mm carapace length (CL)) collected in 1987 with a 20 mm mesh scientific trawl net at depth of 450–700 m on a soft and muddy bottom at least 40 km offshore of Livorno [63]. Another specimen, even smaller (11.7 mm CL), was collected in Reggio Calabria, southern Italy, in the early 1900s at a depth of >850 m and deposited in the Zoological Museum of Turin. This early scyllarid juvenile, likely a recent benthic recruit, suggests that the larvae drift large distances before settling as nistos in deeper waters with muddy habitats where they are possibly protected against the more numerous inshore predators. They then migrate as larger juveniles or sub-adults to inshore habitats [63]. Similar suggestions have been made for other scyllarids. A recent study [64] found *Scyllarus* sp. in the guts of deep sea fish which suggests that nistos are settling in deep waters. *Ibacus* juveniles appear to migrate shoreward from offshore waters to recruit into adult grounds [61]. Juveniles appear to occupy a different spatial niche from adults and are far more cryptic than adults because few individuals are found that are smaller than 20 cm TL [65, 66]. To obtain sufficient numbers of small individuals, specific sampling techniques must be developed which target the juveniles, which may prove difficult if many of the species have juvenile development in deep, oceanic waters. The exceptional discovery of a juvenile form of scyllarid in the old museum collection of Turin [63] emphasizes the importance of comprehensive surveys of crustacean collections, even old ones, in search for scyllarid life stages.

Gaps in life-history make growth rate determination difficult in most species, except for those that can be cultured with high survival rates or from grow-out studies when sufficient juveniles have been captured. Juveniles of reared *S. nodifer* take ~18 months and 9–10 molts to reach adult size [67]. Other fast growing species include *Ibacus* spp. that reach sexual maturity after four to six molts [68]. Cultured *Thenus orientalis* take about 400 days (19 molts) to grow to a size of *c.* 250 g. [69]. In contrast, 7–8 years are necessary for juvenile *S. astori* to recruit fully into the adult population [65]. Hence, from what little data we have on juvenile life history, it appears that many, but not all, of the commercially important scyllarids are capable of rapid growth.

Arctidinid adults (e.g. *Scyllarides* spp.) are typically large and tag–release studies suggest that adults molt annually (*S. latus*, [70]), although data from *S. astori* populations suggest that molts occur every 18–24 months [65, 66]. Molting typically occurs at night and in cooler to warmer months [71–73]. Softening of the old exoskeleton starts some 10–22 days pre-molt, with hardening being complete 3 weeks post-molt. The entire process takes approximately 7 hours, with lobsters remaining shelter-bound for 5–9 days post-molt [74]. Slipper lobsters do not appear to consume their exuviae since these are generally left outside of shelters [72]. Sex ratios are close to unity in those species that have been adequately sampled (*S. latus*, [26, 72]; *S. astori*, [65]). In some species, mean CL is larger for females than for males (*S. latus*, [26, 74]), while in others, males exceed females in size (*S. astori*, [66]). Shortly after mating, females extrude a large number of eggs (conservative numbers range from 24,710 to 356,000), based on TL of the individual, with those eggs ranging from 0.6 to 0.7 mm diameter [26, 66, 75–77]. In some species, spawning occurs twice a year [76]. Such high fecundity rates may be an adaptation to oceanic loss of larvae and variable recruitment of nistos due to cyclic changes in oceanic climate [29]. Eggs are brooded for 2–8 weeks before release over a number of days (*S. latus*, [74, 78]). Ovigerous females are more commonly sampled in cooler months, but not warmer months [66]. There is some evidence that females may return to inshore reefs in the autumn earlier than males and leave sooner after shedding eggs in the mid-summer, possibly to maximize thermal regimes for developing embryos [79]. Most species appear to move to colder, deeper waters when inshore water temperatures rise steeply in the summer or, for those species that remain in lagoons, stay at locations where thermal regimes are less than 25°C [65].

*Ibacus* sp. adults rarely exceed 20 cm TL [1] and are thus smaller than the adults of subfamily Arctidinidae. Sex ratios of all four Australian commercially caught species of *Ibacus* are approximately 1:1. Males are smaller than females because they molt less frequently after attaining sexual maturity. Mating occurs when the female is hard-shelled. Fecundity is much lower than in members of the subfamily Arctidinidae and it is highly variable both within and among the four species of *Ibacus*. It increases with the size of the animal [68]. Egg incubation times have been estimated to vary between approximately 2–4 months and are likely to be temperature dependent with longer incubation in cooler water [61]. Molt frequencies of captive lobsters suggest seasonal molting but wild, tagged lobsters were caught repetitively in consecutive years without having increased in size [68]. Growth models for *I. peronii*, suggest the potential for this species to live for more than 15 years with a maximum size reached after 5–8 years [80].

Very little information is available on adults of *Parribacus* spp. and what does exist is mainly focused on *P. antarcticus*. Two captured females of this species bore evidence of reproductive activity during summer (July) [81].

In *Thenus* spp. growth is quite rapid with 80% of maximum size reached by 2 years of age. Females appear to attain larger sizes than males as evidenced by fishery sampled size ranges in both Indian and Australian waters [82]. Increased

abdominal dimensions likely explain the greater weight of females, while maximization of reproductive efficiency via larger size and the ability to carry more eggs explains the greater mean size of females [83]. However, the two sexes eventually grow to a similar size [84]. Differences between Indian and Australian populations of thenids may reflect differences between sub-species or even between different species in view of the recent taxonomic revision of the genus [4].

In the *T. orientalis* fisheries off India, sex ratios are 1:1 [85], but off Australia they are skewed toward males [83] with a ratio of 0.57. In contrast, *T. indicus* sex ratios are at 1:1 throughout the year [83]. As with all scyllarids, fecundity of thenids scales with length. Various studies in India and Australia show at least two annual spawning periods [83, 84]; however, only a single spawning period was reported for *T. orientalis* off the Tokar delta in the Red Sea [84].

Adults of the subfamily Scyllarinae are usually small and information is very limited regarding growth and reproduction. *Scyllarus arctus* appears to have a continuous reproductive period where females can spawn up to three times per year [10]. The sex ratio is skewed toward females and mean size is larger in females.

## 4. Genetics and population continuity

The developmental period for scyllarid phyllosomas is far more variable than that for palinurids, and can last from a few weeks to at least 9 months [29, 30]. Lengthy duration of the larval period likely leads to wide oceanic dispersion and, ultimately, connectivity of geographically distant subpopulations resulting in panmixia in adults. Molecular tools are just starting to be used to examine population structure of individual species. In one such study, *S. latus* collected in 2 locations in the Western Mediterranean and 13 locations in four regions in the NE Atlantic, including Southern Portugal and the Macaronesian archipelagos, revealed genetic homogeneity in *S. latus* across all regions [86]. More such studies in other species are needed to understand the population genetics of scyllarid species.

## 5. Behavior

Except for *Scyllarides latus* and *Thenus orientalis*, both of which are readily held in laboratory settings, behavior of most slipper lobsters has not been well studied. In addition, the sensory modalities used for behaviors are not well understood as they are in nephropid and palinurid lobsters [87].

### 5.1 Feeding behavior

Feeding behavior of adults is dependent on the structures with which lobsters can capture, manipulate, and process their food and differs with life history stage as mouthparts, pereiopods, and the proventriculus gain substance and size. Feeding habits, primarily for the adults of *T. orientalis* [88] and *I. peronii* [89], and *Scyllarides* spp. [90] are known.

As in clawed and spiny lobsters, the esophagus of slipper lobsters is short, presumably to allow for rapid ingestion [57]. This structure leads into the proventriculus, which is divided into the anterior cardiac stomach and the posterior pyloric stomach. The gastric mill of slipper lobsters is smaller and less calcified [88] likely due to the diet specialization that has occurred in slipper lobsters—that of primarily consuming bivalve flesh, or other fleshy items. Food proceeds from the cardiac stomach to the pyloric stomach through a cardio-pyloric valve, which lacks

the spines and accessory teeth seen in other decapods [88]. Dense mats of setae in the pyloric stomach provide filtering of semi-digested food particles with only the smallest particles entering from the cardiac stomach and exiting into the digestive gland. Larger particles are passed into the midgut caecum and hindgut [88]. Little is understood about the digestive enzymes involved in food breakdown [57].

Many slipper lobsters (e.g. *Scyllarides* spp.) are bivalve specialists and these have evolved the ability to use the nails of their pereiopods to shuck bivalves [90, 91]. During the feeding sequence, slipper lobsters typically probe the outer valves with their antennules, as though "smelling" and assessing the shell for its possible value [92]. They then pick up and hold the bivalve with either the first, third, and fourth or second, third, and fourth pairs of walking legs, using the dactyl tips of the first or second walking legs to repetitively probe the valve edges [92]. The dactyl tips eventually wedge into the shell edge and then push in further and further to open the valves; this process is known as "wedging" [90]. Once the valves are opened enough to fully insert one pair of pereiopod dactyls, another pair of walking legs (second or third) are used to cut the mantle tissue along the pallial line. The lobster then uses a back-and-forth "scissoring" type motion to increase the opening angle to reach the adductor muscles [92]. The second pair of walking legs cut the adductor muscles, so that the valves open freely. With the valves open, the meat is repetitively scraped out of the valves and passed directly to the third maxillipeds [90, 92]; see **Figure 5**. Until the flesh is actually passed back to the third maxillipeds, the antennules make repeated downward motions to probe inside the valves, to touch the flesh, and to touch the shell as the legs scrap the flesh from it; it is likely that the antennules act as a dual "smell" and "taste" sensory modality due to the damage to pereiopod setae from the process of shucking [92].

While bivalves are a preferred food source, slipper lobsters are also known to consume sea urchins, crustaceans, sponges, gastropods, barnacles, sea squirts, algae (*Ulva* spp.), and fish [66, 93]. Gut contents of commercially fished *T. orientalis* in India included a high proportion of mollusks (27.7%) followed by bottom sediments (24.1%), fishes (22.9%), crustaceans (10.7%), polychaetes (4.2%) and miscellaneous food items (10.4%) [84]. Scallops, goatfish and shrimps were always consumed when offered under laboratory conditions [83]. Thus, based on stomach contents and laboratory behavior, *T. orientalis* appears to be an opportunistic,

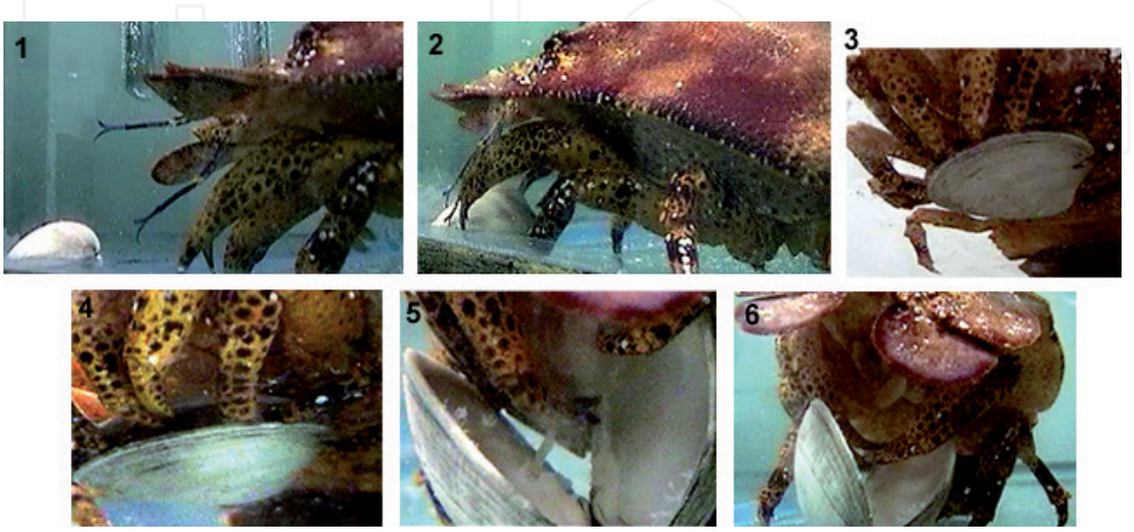


**Figure 5.**
*The feeding sequence of S. aequinoctialis. (1) Lobster approaches bivalve with antennules flicking and sampling odors; (2) pereiopods grab bivalve while antennules "taste" it to assess if feeding sequence will continue; (3) "wedging" of pereiopods into closed valves; (4) probing and "shucking" of the valves, while cutting adductor muscles; (5) close-up of pereiopods ripping adductor muscle; (6) scraping of flesh out of bivalve and delivery to mouthparts.*

omnivorous, benthic feeder that burrows in soft and sandy mud, engulfs sediments consisting of sand and mud, and then preys on organisms that it encounters in this way [84].

### 5.2 Sheltering behavior and substrate preferences

Adult specimens of *Scyllarides* spp. are camouflaged to a certain extent due to their flattened morphology and coloration that blends into hard substrates (e.g. [72, 94]). However, in the brightly illuminated water of their shallow habitats, this camouflage provides only limited concealment against diurnal predators. Thus, most are nocturnal, foraging at night and sheltering during the day ([66, 95, 96] for *S. astori*; [72] for *S. latus*). A more recent set of lab studies documented that *S. latus* is more active at higher temperatures, and demonstrated that warming water temperatures elicited markedly longer movements [97].

Gregarious sheltering has been noted for *S. latus* (Spanier, personal observation) but predation studies at field sites demonstrate that grouping does not decrease per-capita predation rates on individuals within the group. Grouped lobsters suffer an equal rate of predation as lone animals and gain only a small advantage of time, as predatory attack patterns are less focused when lobsters are grouped [98]. Reports of gregarious behavior also exist for *S. nodifer* [99], but nothing is known about the function of such behavior.

The adults of many species are found on hard and soft substrates (**Figure 6**). *Scyllarides* species sampled both on hard (rocks, caves, coral heads) and soft substrates often result from circumstances where lobsters that usually shelter in hard substrates were collected in soft substrates during their short and long term movements, but some species such as *Scyllarides elisabethae*, *S. nodifer*, and *S.*

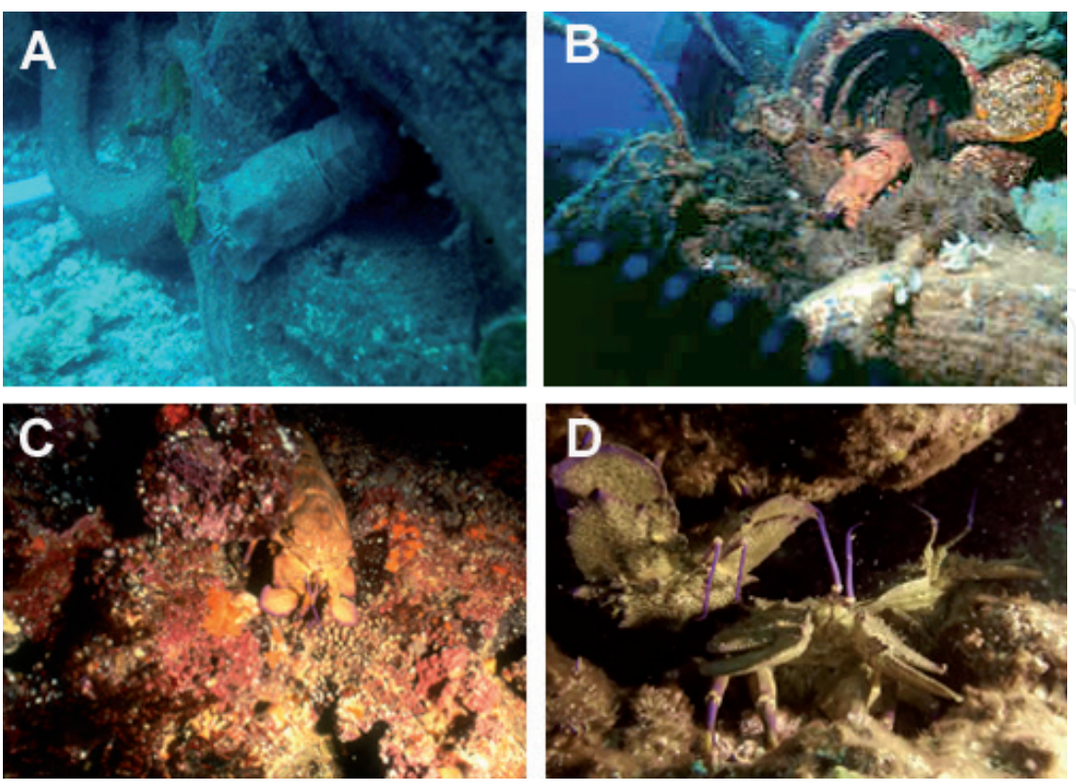


**Figure 6.**
*Scyllarides latus in artificial reef structures (A, B) and natural rock outcropping (C, D). In natural outcroppings and large openings in artificial reefs, they typically co-habit space with other conspecifics (B, D). Photographs by Stephen Breitstein.*

*aequinoctialis* are only found in mud or sand [1, 99, 100]. *Parribacus* species also inhabit hard substrates (corals structures, caves) or are found in sandy bottom [1, 81]. All five species of *Thenus*, and eight species of *Ibacus* inhabit relatively soft sandy or muddy substrates [4, 68] and are well-adapted for digging into the substrate in terms of their morphology as well as their behavior. *I. peronii* spends most of the day underneath the sand [101] and both *T. indicus* and *T. orientalis* spent daytime hours buried in sediment with only eyes and antennules exposed [83], but were nocturnally active, with clear peaks in activity at dusk and just prior to dawn.

### 5.3 Predators and antipredator behavior

The response of slipper lobsters to predator attack (e.g., by gregarious triggerfish) has been well studied [79, 98, 102–108] and consists of three strategies, two of which are typically executed in sequence: (i) the "fortress strategy" in which the animal grasps the bottom and attempts to outlast its attacker's motivation to penetrate its hard shell (described in [107]); (ii) the "swimming escape" response (described in [102, 105–107]); and (iii) remaining sheltered in dens [79, 103]. Lacking claws (like *Homarus* spp.) or long spinose antennae (like spiny lobsters; see [109–112]) with which to fend off swimming predators, slipper lobsters have developed a shell that is thicker and more durable to mechanical insult than clawed or spiny lobsters [107]. They use their short, strong legs to grasp the substrate and resist being dislodged [105, 106] (see **Figure 7**), and if this fails, they are exceptionally deft swimmers capable of evasive maneuvers [102]. Also they may suddenly change the direction of their swimming, presumably to confuse the chasing predator. This is an energetically costly response to a threat and is generally used as a last resort. Slipper lobsters may match the energy invested by clawed lobsters in claws and spiny lobsters in antennae by increasing only moderately the thickness of their shells and bettering their swimming escape behavior [107].

Slipper lobsters that live in complex substrates also display a variety of shelter-related behaviors that provide a third highly effective survival strategy [105]. By combining nocturnal foraging with diurnal sheltering, as well as carrying food to their shelters for later consumption, slipper lobsters may fully minimize their exposure to diurnal predators. The tendency for cohabitation with conspecifics (as seen in *P. antarcticus* [1, 81] or *S. latus* [98]) may be adaptive because of confusion effects (which lobster to target), alerting earlier to predators due to higher levels of "prey vigilance", or being concealed among conspecifics ("dilution effect" *sensu* [113]; see **Figure 7**). If these tactics fail, their thick carapace effectively blunt cracks [107, 114, 115] and may buy them extra time for escape when attacked.

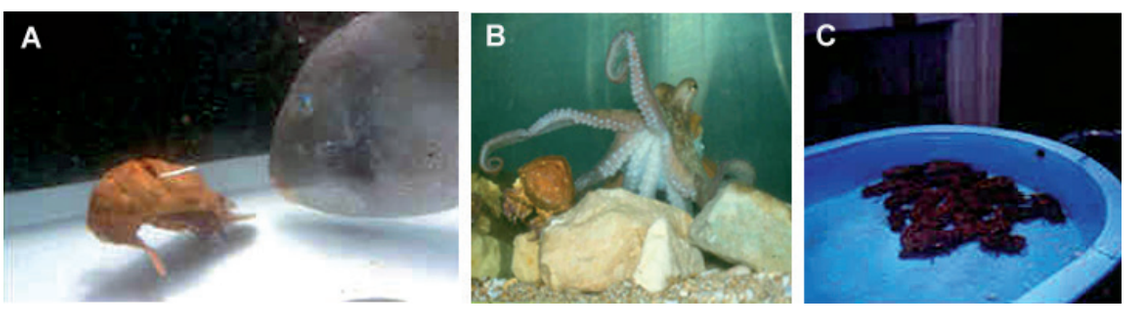


**Figure 7.**
*Anti-predator responses of Scyllarides latus. (A) Tail flip in response to on-coming threat by triggerfish; (B) wedging into rocks in response to a predator (such as octopus) that can grip; (C) gregarious behavior in absence of shelter where each individual is concealed among other conspecifics. Photographs by Ehud Spanier.*

Very little is known about the antipredator behavior of soft bottom species. Fully buried *Thenus* spp. are entirely concealed except for the eyes and antennules [83]. *Ibacus* spp. also are found on soft bottom substrates and are known to bury into those sediments, much in the same manner as *Thenus* spp. [68, 101] presumably also for concealment.

Besides triggerfish, spotted gully shark (*Triakis megalopterus* (Smith, 1849) have been reported to feed on *S. elisabethae* in South Africa [116], groupers (*Epinephelus* and *Mycteroperca* spp.) have been reported as predators of adult and juvenile *S. latus* [26] and *S. arctus*, *S. aequinoctialis*, and *S. nodifer* [56, 117]. Combers (*Serranus* spp.) and rainbow wrasse (*Coris julis* Linnaeus, 1758) apparently prey on juvenile *S. latus* [26]. Juvenile *S. aequinoctialis* were found in the gut of a large invasive alien red lionfish (*Pterois* spp.) in Belize [118].

### 5.4 Mating behavior

Most information on reproductive behavior comes from laboratory observations. Unlike clawed lobsters where mating usually occurs shortly after females molt, scyllarids are more similar to palinurids in that mating and molting are separate and unrelated events, although in the hooded slipper lobster (*S. deceptor*), copulation follows molting [119]. The general decoupling of molting and mating is largely due to males supplying females with external spermatophores that females use within hours or a few days. Nevertheless, some differences exist among the different subfamilies and those are summarized here. Males of *Scyllarides* spp. produce white, gelatinous spermatophores, which they carry around on the base of their fourth and fifth pereiopods ([74]; Spanier, personal observations) and transfer to females. In some species, females have been observed carrying spermatophores externally 6–10 days prior to egg extrusion (*S. latus*, [26, 74]), while in others, the lack of observable spermatophores prior to egg extrusion has led to a belief that the spermatophore is stored internally and fertilization is internal (*S. nodifer*, [55]; *S. squammosus*, [120]). Females of many species can spawn multiple broods in a season due to short brooding periods, and these broods are usually carried during spring and summer months. Only in *S. latus* have both eggs and spermatophores been observed simultaneously [74].

Male *Thenus* spp. do not appear to deposit a persistent spermatophoric mass in the process of mating [83]. Soft, non-persistent masses were observed [121] for *T. orientalis* and females oviposited within 8 hours post-mating and lost the spermatophore within 12 hours. No courtship behaviors or acts of mating have been witnessed in *Thenus orientalis* or *T. indicus* during 2000 hours of remote video observation [83], so it assumed that mating rituals are very simple. In *Ibacus* spp. spermatophoric masses were persistent, gelatinous, and opaque white in color, and were deposited in two elongated strips, approximately 20–30 mm long, close to the genital openings of the female [68]. Fertilization is likely external and occurs relatively soon after mating.

From the very limited information available on *Parribacus* spp., it appears that spermatophores are persistent even after spawning and new spermatophores are deposited atop old ones [81].

In *Scyllarus* spp. males deposit two jelly-like strings of spermatophores ventrally from the base of the fifth pereiopod to the second abdominal segment; these are used within hours to inseminate eggs and any remaining sperm mass degrades quickly [10]. Females are capable of multiple spawning events per year, but the number depends largely on environmental conditions; members of the same species may produce three broods in one area, but only two in another. This flexibility in

reproduction may prove advantageous when thermal regimes are favorable for rapid gonadal maturation, shorter incubation periods, or rapid larval development [10].

### 5.5 Movement patterns

Slipper lobsters movements consist of either slow, benthic walking used for daily nomadic movements within a small home range and for seasonal migrations from shallow inshore waters to deeper offshore waters or swimming movements that are used for escape or vertical migratory movements. Daily activity patterns suggest that slipper lobsters have endogenous clocks that provide for circadian rhythms with higher locomotor periods during night hours [122]. Tagging studies of *S. latus* off the coast of Israel confirm the slow, benthic walking patterns: local movements within a home range, presumably to forage and migratory offshore movements [79]. While residing inshore (February to June in the south-eastern Mediterranean), lobsters make short-range movements from reef shelters to forage and 71% return to these reef shelters. However, lobster numbers decreased in the reef shelters, ultimately decreasing to zero in summer months (June through August), and lobsters did not return to the reef until the following winter when their numbers peaked in the spring. This suggests a migration offshore that would correspond to increased water temperatures inshore [79]. Similar tagging studies off Sicily showed no such migratory movements [70]. *Scyllarides squamosus* also appears to make no long-range migratory movements, with mean distances moved from tagging location by most (97.2%) individuals being <1 km over a 5 year period [123].

Mobility of *Thenus* spp. in Australia also has been examined through use of tag and recapture studies and monitoring of commercial catch levels [83, 84]. *Thenus* spp. tend to be very mobile and capable of moving large distances, but because their movements lack any kind of pattern or directionality, they are not likely to be migratory. Likewise, *Ibacus* spp. exhibit nomadic movement patterns that have no directional patterns [124].

Swimming behavior constitutes a form of locomotion in which a single "appendage"—the abdomen—produces thrust by a combination of a rowing action and a final "squeeze" force when the abdomen presses against the cephalothorax [125]. Although the tail-flip response is known in adults and juveniles of all three major taxonomic group of lobsters, it is best developed in slipper lobsters.

The hydrodynamics of swimming in slipper lobsters has been studied in *Ibacus peroni*, *I. alticrenatus* [101, 126–128], *Thenus orientalis* [83, 126, 127, 129] and *Scyllarides latus* [102, 130, 131]. *S. latus* uses a "burst-and-coast" type of swimming in response to a threat. This burst-and-coast swimming consists of large amplitude movements of the abdomen followed by periods of powerless gliding. Acceleration can reach top velocities of three body lengths per second while deceleration during gliding decreases to velocities of less than one body length per second. Escape swimming is of short duration used only in emergencies to get to safety, as it requires considerable energy. The flattened second antennae of *S. latus* (mistakenly called "shovels" or "flippers"), with their movable joints, serve as stabilizers or rudders to control the swimming movement [130]. This adjustment in lift via the second antennae is also seen in *Ibacus* spp. and *Thenus* spp. [127].

In *Thenus* spp., there are two distinct forms of swimming: a locomotory form that is characterized by a slower speed (average of 29 cm $s^{-1}$) and the absence of explicit stimulus, and escape swimming which is much faster (average of 1 m $s^{-1}$), similar to that seen in *S. latus*, and always caused by direct stimulus or threat [83, 129].

In locomotory swimming, the aerofoil body shape generates lift as the abdomen thrusts downward; drag is reduced by all pereiopods being extended anteriorly [127]. Lift height was controlled by the second antennae and each flexion helped to maintain the animal above the sediment [127, 129]. In comparison, escape swimming always consisted of an abdominal flexion that was proportional to the magnitude of the stimulus. While *Ibacus* spp. can tail flip, it does not do so in response to a sudden threat, but seems to be related more to a righting response when the animal is flipped over [128].

## 6. Diseases

There are only a few reports on diseases or parasites of slipper lobsters, in general, and of specific species in particular [132, 133]. This limited information is usually focused on commercial species and those that have potential in aquaculture. *Scyllarides* specimens die while being held in the laboratory from unknown causes. Halacarid mites, *Copidognathus* spp., cause tissue necrosis in the gills of the *P. antarcticus* [133]. Aquaculture of *Thenus* spp. and *Ibacus* spp. will require more knowledge on pathogens of these species since the phyllosomas are very susceptible to microorganisms in the water column [69, 134]. There are also reports of parasites in adults. For example, a new species of parasitic copepod, *Choniomyzon inflatus* n., has recently been collected from the external egg masses of the smooth fan lobster *Ibacus novemdentatu* [135]. The Gram-negative *Vibrio* causes mass mortality during hatchery production of phyllosoma larvae and also affects their live feed of *Artemia* nauplii. Filamentous bacteria (*Leucothrix* sp.) and protozoans (such as *Zoothamnium* spp., *Vorticella* spp. and *Acinata* spp.) can also biofoul the phyllosomas and cause mortality [8]. Traditionally, a number of antibiotics as well as other chemicals have been heavily used for controlling bacterial colonies in the rearing water. Alternative methods are the use of ultraviolet light (UV) and ozone ($O_3$) sterilizers [8, 69].

## 7. Environmental effects and conservation

Overfishing, climate change, and habitat degradation are the main reasons for the drastic decline of marine populations over the past 30 years [136]. The effects of overfishing characterize many populations of commercial slipper lobsters and result in decreases in exploited stocks in the last few decades. Some species of slipper lobsters, formerly ignored, are now targeted due to the decline in other species (e.g., spiny lobsters) especially around the waters off Australia, Hawaii, India, the Galápagos Islands, and the countries surrounding the Mediterranean Sea. As a consequence, slipper lobsters have rapidly decreased in stock abundance to the point that local fisheries have collapsed [7]. Regulations established that try to protect these populations may have unexpected negative effects. For example, the prohibition against landing ovigerous females of *Scyllarus arctus* in NE Spain has biased the fishery toward males [10], which then affects natural sex ratios, opportunities for females to find mates, and ultimately population structure. Protected natural reserves/no-take zones can, to a certain extent, help rectify these effects [137], but require governmental action and policing. A fully protected, natural reserve off the northern Mediterranean coast of Israel has demonstrated significantly higher numbers of female and male *Scyllarides latus* compared to a control area with the same characteristics [138]. The specimens in the reserve were also significantly larger than those in the control, non-protected area.

Instead of regulations that may have unintended consequences or the creation of natural reserves that require political will, policing, and industry buy-in, targeted fishing moratoriums may also help to rebuild stocks. For example, depleted stocks of *S. elisabethae* recovered during a six-year moratorium from fishing and trapping off eastern South Africa [139]. However, despite years of protection, populations of *S. squammosus* in the Northwestern Hawaiian Islands, have failed to recover [140]. Possible factors that may limit population growth and recovery, include: climate change, Allee effects, and interspecific interactions. Community changes that come from overfishing of coral reef fauna might have broad and lasting results; once lost, valuable resources and ecosystem services may not quickly rebound to pre-exploitation levels and may have cascading effects on the larger fauna that rely on these resources [140]. Projected climate change impacts on the distribution of coastal lobsters, including a synthesis of 68 slipper lobsters species, suggest negative changes in diversity in areas of high commercial fishing due to habitat loss [141]. Such changes are expected to be particularly dramatic in the tropics, with species projected to contract their climatic envelope between 40 and 100% [141].

## 8. Conclusions

Although slipper lobsters represent the most speciose group of lobsters and have been exploited in targeted or by-catch fisheries, they have been and continue to be poorly studied compared to the less speciose but more popular clawed and spiny lobsters. Lack of knowledge of basic biological features such as life history, behavior, physiology, and disease does not bode well for the long-term health of populations especially when most scientists expect dramatic climatic changes to impact oceanic habitats and community structure. Given that these lobsters represent a potential food source for an ever-growing human population, it would be beneficial to understand much more about these lobsters with targeted studies, supported by governmental agencies, much as we saw for clawed and spiny lobsters nearly 40 years ago.

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